ONTOGENY OF DISPLAY IN IMMATURE
SCHIZOCOSA CRASSIPES (ARANEAE: LYCOSIDAE)

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Most studies dealing broadly with behavioral ontogeny in spiders have been concerned with orb-weaving (Witt and Baum, 1960; LeGuelte, 1969; Peters, 1969; Reed, Witt, Scarboro and Peakall, 1970). However, relatively little attention has been directed to the ontogeny of display. Immature lycosid spiderlings do not exhibit the complex stereotyped displays typical of adult wolf spiders during courtship (Rovner, 1968) or agonistic encounters (Aspey, 1974, 1975). Crane (1949) reported that several species of immature salticid spiders occasionally performed abortive displays, but she considered such displays exceptions to the rule. Rovner (1968) looked unsuccessfully for courtship display in penultimate male *Lycosa rabida;* the tendency to court did not appear until several days after the final molt. The first study of display ontogeny in spiders was that of Dijkstra (1968, in Koomans et al., 1974), which was expanded by Koomans, van der Ploeg and Dijkstra (1974) who observed a characteristic "leg wave behavior" in a variety of subadult *Pardosa* spp. This behavior was observed from the second instar to the adult molt in *P. lugubris* and *P. nigriceps,* and decreased in frequency with concomitant increases in courtship.

In considering the functional significance of leg wave behavior, Koomans et al. (1974) suggested that courtship replaced the behavior in adult males, while in adult females, the behavior was probably replaced by specific reactions to courtship. Dijkstra (1968, in Koomans et al., 1974) observed similar leg movements in juvenile *P. amentata,* but the behavior was not restricted to courtship situations. Van der Ploeg (personal communication) has observed leg waving in immature *P. purbeckensis* in the field. Similarly, I had observed (Aspey, 1974) that both male and female *Schizocosa crassipes* (Walckenaer) exhibit a characteristic leg wave display as juveniles.

In extending the generality of leg waving display among immature lycosids, this study describes the ontogeny of leg wave display among immature *S. crassipes* and suggests a biological significance for the behavior.

METHODS

The subjects were 64 immature *S. crassipes*. Thirty-two spiders (16 males and 16 females) were collected during early May, 1971-73, as antepen- or penultimate instars from Stroud's Run State Park, Athens Co., Ohio, USA. The remaining spiderlings were reared from laboratory-mated adults. These spiderlings were observed from egg case emergence (considered the second instar) until approximately 1 wk after dispersal from the female. For most spiderlings, one additional molt (to the third instar) occurred in the laboratory, but too few animals survived beyond this time to continue observations. However, observations continued until the final molt for those spiders collected as antepen- and penultimate instars in the field. Data are reported only for those individuals for whom sex was correctly established at the antepen- or penultimate instars.

Six antepen- and penultimate spiderlings of each sex collected from the natural habitat and 12 laboratory-maintained spiderlings were isolated in covered clear plastic containers (12.5 × 7.0 × 7.0 cm). One-half of these spiders were visually isolated, while the remaining containers were adjacent and allowed the spiders visual access to one another. Ten antepen- and penultimate spiderlings of each sex collected from the field were socially housed (sexes separate) in glass terraria (26 × 19 × 22 cm) fitted with plastic covers.

Two groups of laboratory-maintained spiderlings (10 per group) were observed during their second and third instars. In order to observe these animals under the above conditions, spiderlings were brushed off the female's abdomen with a camel hair brush. Ten individuals were then placed in an observation chamber identical to the one in which socially grouped antepen- and penultimate instars were maintained. At the conclusion of each observation period the spiderlings were returned to the female and allowed to regroup. After dispersal from the female began, two groups of 10 individuals were transferred to separate observation chambers until the third instar, at which age observations were terminated.

The frequency (i.e., bouts per 30 min) and duration of leg waving were recorded for 30 min daily with a manually activated Ester-

line-Angus event recorder (chart speed of 15.2 cm/min). Total observation time varied according to whether the subject reached sexual maturity or died at a previous instar. The temporal patterning of leg waving from six laboratory-maintained spiders during the antepen- and penultimate instars was also recorded. Protocol was whispered into the microphone of a tape recorder. These recording instruments were placed on a separate table from the observation chambers to minimize the effects of machine vibration.

Vestigial-winged *Drosophila melanogaster* were offered as food to each spiderling once weekly, and a constant water supply was available. The spiderlings were maintained and observed under relatively constant temperature (22-26°C) and humidity conditions (55-62% RH).

Results

Leg waving display in immature *S. crassipes* consisted of the simultaneous raising and lowering of the first and second ipsilateral legs. Leg waving was generally performed at a steady and smooth rate, and not alternated from side to side during a leg waving bout. Spiderlings showed no preference for either the right or left side during leg waving. Although leg waving occurred nearly as often per 30 min during all instars, no consistent temporal patterning was evident until the antepen- and penultimate instars, at which time leg waving became increasingly stereotyped and sexually differentiated.

Leg waving was observed only five times in the 24 socially isolated spiderlings. Four of these instances were limited to those spiders having visual access to one another, while only one visually isolated spiderling exhibited leg waving. The five observations of leg waving occurred in females once each at the second, third, and antepenultimate instars, and in males twice during the penultimate instar.

Although leg waving was rarely observed in socially isolated spiderlings regardless of age or sex, socially grouped spiderlings of both sexes at all the developmental stages studied exhibited leg waving. With regard to the frequency of leg waving as a function of age, no differences were evident in the average frequency of leg waving/30 min among the four developmental stages (second instar: 19.7 ± 9.6 SD; third instar: 21.2 ± 6.3 SD; antepenultimate instar: 19.8 ± 5.1 SD; penultimate instar: 22.2 ± 6.7 SD). Considering

leg waving as a function of sex, antepen- and penultimate males exhibited higher average frequencies of leg waving/30 min (27.2 ± 7.0 SD) than females (12.4 ± 4.0 SD) (Mann-Whitney U = 18, p < 0.02).

Of the 10 males and 10 females collected from the natural habitat and grouped separately by sex, nine males and four females reached sexual maturity. Cannibalism among these spiders was directly observed on two occasions; the remaining deaths may have been due to other causes. In the two groups of 10 laboratory-maintained juveniles, two individuals from each group reached the fourth instar. Among these spiders cannibalism was also directly observed on two occasions.

Among socially grouped antepen- and penulatimate males, bouts of leg waving lasted an average of 7.3 ± 2.1 (SD) sec, and consisted of the legs being waved 3-27 times ($\bar{x}$ ± SD: 16.0 ± 4.7) in succession at a rate of approximately 2 waves/sec. With increasing age, film analysis revealed that the foreleg was lifted higher off the substratum (20-25° in the second and third instars) until an arc 40-50° relative to the substratum was reached in the antepen- and penultimate instars. The second ipsilateral leg that accompanied the foreleg during leg waving was lifted only 5-25° relative to the substratum. The legs were raised and lowered almost simultaneously, with the foreleg occasionally leading.

Among socially grouped antepen- and penultimate females, bouts of leg waving lasted an average of 4.1 ± 2.0 sec, and consisted of the legs being waved 1-10 times ($\bar{x}$ ± SD: 3.0 ± 2.2) in succession at a rate of approximately 1 wave/sec. Although females exhibited leg waving more slowly and less frequently than males, the behavioral topology of leg waving was indistinguishable between the sexes. Bouts of leg waving alternated with variable periods of immobility or locomotion, and depended on the behavior of conspecifics.

The circumstances under which leg waving occurred did not seem to change with age. A spiderling initiated leg waving in response to a darting front approach by a conspecific when it approached to within two or three body lengths. In response to one or several bouts of leg waving, the approaching spider turned away and/or retreated. On the four occasions when cannibalism was observed, the cannibalized spiderling was approached from the posterior; leg waving was not observed to occur in response to these posterior approaches.

Discussion

Observations on the ontogeny of display in *S. crassipes* provide an interesting contrast with those of Koomans et al. (1974) for *Pardosa* spp., although certain similarities exist. For example, in both sexes of the *Pardosa* species, the pattern of leg wave behavior was generally the same at all developmental stages, with the frequency decreasing rapidly at the adult molt. In *S. crassipes* leg waving patterns become increasingly stereotyped with age, but the frequency did not vary with age or decrease as the final molt neared. Blinded *Pardosa* showed relatively little leg wave behavior, similar to the lack of leg waving exhibited by socially isolated *S. crassipes*. Although both sexes of *Pardosa* spp. and *S. crassipes* exhibited leg waving, antepen- and penultimate male *S. crassipes* displayed significantly more than females. Of further interest were the findings that bouts of leg waving by males lasted longer and consisted of more waves than those exhibited by females. These findings, coupled with the observation that more males than females reached sexual maturity among socially grouped spiderlings, suggested that leg waving serves a communication function that becomes more sexually differentiated with age. This idea is consistent with Aspey's (in preparation "a," "b," "c") research that only adult males exhibit the highly complex agonistic display which serves to maintain dominance-subordinance relations and preserve inter-individual distances.

The decrease in leg wave behavior concurrent with increased courtship by adult male *P. lugubris* and *P. nigriceps* suggested to Koomans et al. (1974) that the behavior was replaced by courtship. Analogously, leg wave behavior in adult females could be replaced by specific reactions to courtship. In immature *S. crassipes* leg waving may be homologous with the similar ipsilateral Prolonged Wave in adult males (Aspey, 1974, in preparation "a"). Although Prolonged Wave occurred infrequently in adults relative to the frequency of immature leg waving among socially grouped spiderlings, both behaviors occurred under similar circumstances (i.e., one spider approaching another from the front). These behaviors seemed to have similar behavioral consequences, that of increasing distance between two individuals and thwarting approaching conspecifics.

Koomans et al. (1974) suggested that since leg wave behavior is similar in most *Pardosa* species observed, it may serve as a signal in agonistic encounters between individuals of different sympatric species, as well as between conspecifics. Just as one of the functions of courtship is the suppression of predatory tendencies, experimentally

demonstrated in jumping spiders by Drees (1952), a similar inhibition of agonistic responses may also be the role of leg wave behavior.

Leg waving probably is a mechanism to space spiders living in dense populations; this would minimize cannibalism and competition for food supplies. Observations on immatures and adults support this idea. The only occasions during which observed cannibalism occurred among immatures was during a posterior approach when leg waving did not occur. The probability of cannibalism is likely minimized during a face-to-face encounter when the approached spider exhibits leg waving, and the approaching spider subsequently retreats.

Although immature *S. crassipes* exhibit the various locomotory and contact behaviors of reproductively mature adults (Aspey, 1974, in preparation "a"), adult-like foreleg movements and postures are not observed until sexual maturity. The complex, stereotyped agonistic display of adult male *S. crassipes* serves to determine dominance-subordinance relations (Aspey, in preparation "b"), as well as space the animals according to a specific inter-individual personal distance (Aspey, in preparation "c"). The prominent tibial brushes of adult males, coupled with foreleg movements, probably serve as visual signals to indicate the presence of male conspecifics. However, with immatures, tibial brushes are lacking, and leg waving is probably the only visual signal available; it may serve a generalized spacing function for immatures of both sexes until the various adult behaviors develop. Thus immature leg waving may be considered a mechanism to space spiderlings, with the added consequence that cannibalism is minimized and spiders are selected against that do not exhibit and/or respond appropriately to leg waving.

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